

Primary inhibition by light: A unique property of bivalve photoreceptors*

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Abstract: Bivalve molluscs are known for shadow responses involving closure or retraction of the siphon and valve adduction. In representative genera [*Spisula solidissima* (Dillwyn, 1918), *Mercenaria mercenaria* (Linnaeus, 1758), *Lima scabra* (Born, 1778)], the pallial nerves contain photosensitive fibers that exhibit physiological shadow responses. These photoreceptors are inhibited by light but trigger an excitatory burst of spikes to a shadow, the off-response. Equivalent responses are seen in bivalve eyes, e.g., in optic fibers from the siphon tentacle eyes of *Cardium edule* (Linnaeus, 1758) and the mantle eyes of scallops (Pectinidae) and file clams (Limidae). In scallops, they form a distal retinal layer of ciliary receptors, distinct from a proximal microvillar layer that is excited by light. In off-receptors (ciliary), light inhibition is the result of a hyperpolarizing receptor potential with spikes generated on the rebound depolarization at dimming. In contrast, the proximal on-receptors are excited by light with spikes generated by depolarizing receptor potentials. The inhibitory effect is first-order, i.e., a direct response to light, as is excitation for the proximal receptors. With separate retinas and the absence of synaptic contact, these are the primary receptors. Aside from *Pecten Müller*, 1776 and *Lima Bruguière*, 1797, the only other bivalve eyes in which receptor potentials have been investigated are those of the giant clam *Tridacna maxima* (Röding, 1798). Here there are two types of hyperpolarizing, light-inhibited primary receptors, one of which generates spikes at light offset, the other non-spiking. The inhibitory response is universal in bivalve photoreception, unique among the eyes of invertebrates, but similar in polarity to chordate photoreceptors although the ionic mechanisms are different. Receptor physiology is discussed relative to image formation in bivalve eyes.

Key words: shadow response, mantle, retina, *Pecten*, *Tridacna*

The cast of a shadow onto benthic and/or sessile organisms commonly triggers some form of withdrawal into a shell or burrow. Such is the case for most shallow, subtidal bivalve molluscs. In bivalves, this 'shadow response' involves a variety of movements including siphon closure, retraction of the siphon or mantle, and shell adduction (Wenrich 1916). For most bivalves this response does not require eyes. Rather, the mantle tissues themselves are sensitive to light as confirmed in pallial nerve recordings from a number of species (Kennedy 1960, Mpitsos 1973, Wiederhold *et al.* 1973). However, a few bivalve families have added functional eyes ectopically around the shell-mantle edge (Morton 2001). These constitute a well-developed visual system for motion sensitivity that triggers sight reactions independent of direct shadowing of the animal (Nilsson 1994). Most prominent are the distinctive blue eyes of the scallop (Fig. 1), visual organs that have attracted the attention of classical morphologists (Dakin 1910, 1928) to present-day neuroscientists. Morphology and optics have been examined in detail in the eyes of *Pecten maximus* (Linnaeus, 1758) (Dakin 1910, 1928, Land 1965, Barber *et al.* 1967), recently in *Amusium balloti* (Bernardi, 1861), *Argopecten irradians irradians* (Lamarck, 1819), *Chlamys hastate* (Sowerby, 1842), *Chlamys rubida* (Hinds, 1845), *Spondylus americanus* (Herman,

1781), and *Crassodoma gigantea* (Gray, 1825) (Speiser and Johnsen 2008), *Cardium edule* (Linnaeus, 1758), and *Tridacna maxima* (Röding, 1798) (Barber and Land 1967, Kawaguti and Mabuchi 1969, Land 2003, Stasek 1966) to evaluate bivalve vision. Here, physiological properties are examined with emphasis on the unique inhibitory response to light in bivalve photoreception and its role in behavior and visual function.

Light inhibits sensory neurons in the mantle and eyes

Bivalves, alone among the non-chordate invertebrates, have adopted a near-universal inhibitory response to light, a physiological mechanism suitably adapted for the shadow response. Termed 'primary inhibition', activity in photosensory neurons is suppressed by the absorption of light independent of synaptic interactions at the receptor level and therefore a first-order response. Photoreception in chordates is also inhibitory, hyperpolarizing by convention, but with contrasting mechanisms to be considered later. Light inhibition was first observed in optic nerve recordings from scallop eyes (Hartline 1938). Upon dimming these same fibers produce vigorous bursts of action potentials or spikes, the 'off-response'. However, inhibition is also characteristic of the dermal light response in the bivalve mantle. For ex-

* From the symposium "Molluscan models: Advancing our understanding of the eye" presented at the World Congress of Malacology, held from 15 to 20 July 2007 in Antwerp, Belgium. Co-sponsored by the National Science Foundation and the American Malacological Society.



Figure 1. *Argopecten irradians taylorae* (Petuch, 1987) in its shallow-water, turtle grass habitat, St. Joseph Bay, Florida.

ample, the siphonal nerves of the lamellibranchs *Mya arenaria* (Linnaeus, 1758), *Mercenaria* (= *Venus*) *mercenaria* (Linnaeus, 1758), and *Spisula solidissima* (Dillwyn, 1817) each contain neurons whose spontaneous activity is inhibited by light. In *Spisula* this "simple" photoreceptor system (Kennedy 1960) consists of a single pair of siphonal neurons leading to the visceral ganglion where the motor response for siphon retraction is generated. In these neurons, the light response has been characterized as a dual inhibitory-excitatory process involving different photopigments. The response is modeled as the sum of a low-threshold, short-wavelength inhibition and a long-wavelength excitation responsible for the off-response burst of impulses (Fig. 2). The photopigments, as yet unidentified, are assumed to coexist

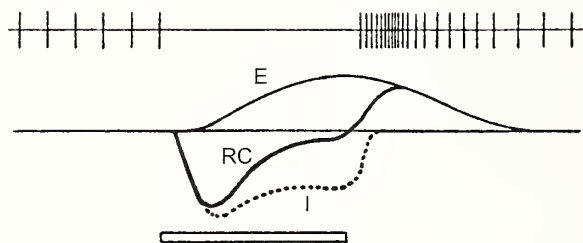


Figure 2. Model of primary inhibition in *Spisula* siphonal neuron. Light (bar) evokes a low-threshold light intensity inhibition (I) and delayed, long-lasting excitation (E) whose sum is the receptor potential (RC) that accounts for the inhibition of spiking and the burst of action potentials at light offset. The inhibitory effect is hyperpolarizing and the excitatory effect depolarizing. After Kennedy (1960).

within the neuron since the light response does not originate from presynaptic receptors. Likewise, photosensory neurons in the siphon nerves of the hard shell clam *M. mercenaria* are inhibited by light, with spikes elicited only in response to dimming (Wiederhold *et al.* 1973). Membranous whorls in the distal portions of these neurons indicate, again, that these neurons contain photopigments and respond directly to light. Mantle neurons in the file clam *Lima scabra* (Born, 1778) also generate off-responses independent of light sensitivity in the eyes (Mpitsos 1973).

Light inhibition in the scallop eye was initially attributed to synaptic interactions in the retina (Hartline 1938), reminiscent of the lateral inhibitory synapses among *Limulus polyphemus* ommatidia well known as the basis for contrast enhancement (Hartline and Ratliff 1958). This interpretation grew out of the fact that the scallop retina contains a dual layer of photoreceptor cells (Fig. 3). Inhibition and the corresponding excitatory off-response are properties of the distal layer, whose ciliary photoreceptors and axons form the distal ramus of the optic nerve. Optic fibers from the proximal, rhabdomeric layer form the proximal ramus and respond to light with an excitatory 'on-response'. Although Hartline favored the interpretation that the proximal receptors were the source of excitation for the off-response in the

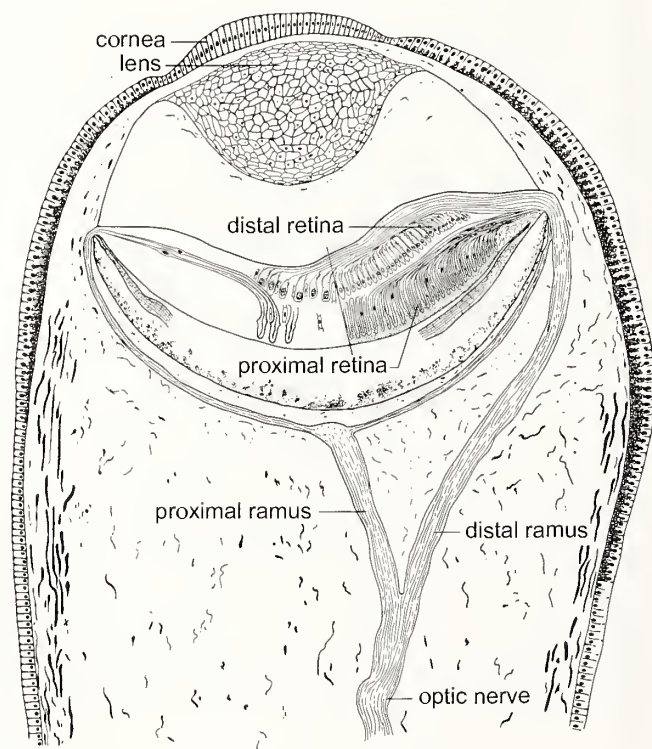


Figure 3. Diagrammatic representation of *Pecten* eye. Modified from Dakin (1928).

distal receptors, the latter equivalent to vertebrate retinal ganglion cells, he also considered the possibility that distal receptors represented a new type of cell, "excited only by the removal of a stimulating agent" (p. 477). The latter interpretation, that the distal receptors are a new type of cell, is now accepted, both for distal receptors in the eye and for photosensory fibers in the mantle. In the eye, ultrastructural examination of the retina has since revealed no evidence for synaptic connections either between proximal and distal layers or among neighboring photoreceptors (Barber *et al.* 1967), thereby ruling out synaptic interactions as the basis for inhibition by light. Unequivocal segregation of proximal and distal responses has also been confirmed by cutting the distal ramus, thereby eliminating off-response activity in the optic nerve (Hartline 1938, Land 1966). With minor differences in spontaneous activity the visual responses are equivalent for all species of scallop. As in scallops, the eyes of *Lima scabra* have a dual retina and on- and off-responses in the respective optic fibers of proximal and distal origin (Mpitsos 1973). Also, ciliary receptors that resemble those in the scallop distal retina are present in the tentacle eyes of *Cardium edule* and spiking in their optic fibers occurs only in response to a decrease in light intensity (Barber and Land 1967).

The inhibitory effect of light in the distal (ciliary) photoreceptors of scallops, along with bivalve siphonal nerves, is unusual considering that a light stimulus to the eyes of most animals is excitatory and triggers bursts of impulses in optic nerve fibers, as in the excitatory on-response in the scallop proximal (rhabdomeric) photoreceptors. An excitatory response, to light or any other sensory stimulus is generated by a depolarizing receptor potential, a reduction in membrane potential toward spike threshold. Impulses arise in response to these depolarizing currents, either at the spike initiation zone of photosensory neurons or in presynaptic non-spiking retinal cells. Hyperpolarization, in contrast, increases the membrane potential away from threshold levels exerting a stabilizing, spike-inhibiting influence. Excitatory, depolarizing receptor potentials in response to light are characteristic of all non-chordate invertebrate eyes examined so far, with bivalve eyes the only exception. Representative examples, based on intracellularly recorded receptor potentials, include annelids (Walther 1965, Fioravanti and Fuortes 1972), insects (Naka 1961), gastropod (Dennis 1967) and cephalopod molluscs (Tomita 1968), and arthropods, as first demonstrated in the horseshoe crab *Limulus polyphemus* (Hartline *et al.* 1952, Fuortes 1959). Each of these 'excitatory' examples represents a phylum or taxon (annelid, gastropod, cephalopod, arthropod) with rhabdomeric photoreceptors. Photosensitive neurons in the arthropod central nervous system are also excitatory, *e.g.*, the crayfish caudal photoreceptor, a photosensory interneuron in the 6th abdominal ganglion

discovered by Prosser (1934) and later shown to be depolarized by light (Wilkins and Larimer 1972). However, exceptions to the bivalve-only inhibitory effect exist if one considers extraocular photosensitivity, *e.g.*, gastropod CNS neurons are inhibited and/or hyperpolarized by light (*Aplysia californica* (Cooper, 1863), Brown and Brown 1973; *Onchidium verruculatum* (Cuvier, 1830), Goto and Nishi 2002; see review of extraocular photosensitivity by Yoshida 1979). In most instances these neurons are neither ciliary nor rhabdomeric.

In bivalves, receptor potentials obtained from intracellular recordings were first observed in photoreceptors from scallop eyes (Toyoda and Shapely 1967, Gorman and McReynolds 1969). Receptor potentials in the distal layer are hyperpolarizing in response to light (Fig. 4B), consistent with primary inhibition and spike suppression previously established for these receptors. At light offset the membrane potential rapidly depolarizes generating the off-response burst of spikes. In contrast, the proximal photoreceptors are depolarizing (Fig. 4A), generating spikes at light onset. Similar hyperpolarizing (inhibitory) and depolarizing (excitatory) responses have been reported for the corresponding retinal receptors in *Lima scabra* (Mpitsos 1973).

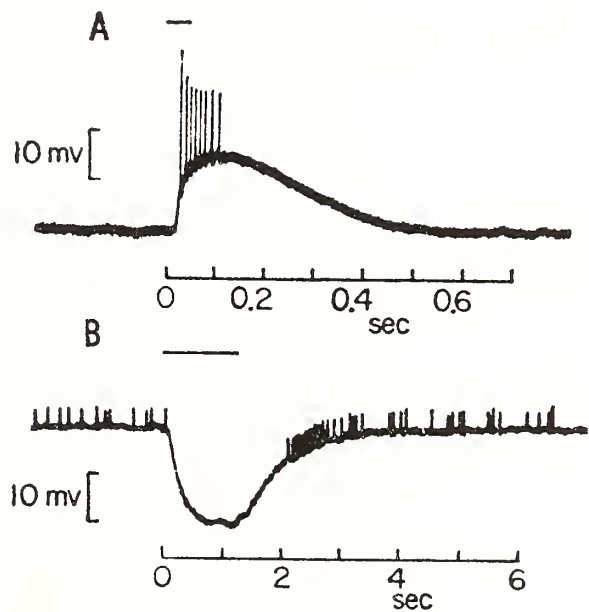


Figure 4. Receptor potentials with accompanying action potentials in excitatory proximal (A) and inhibitory distal (B) photoreceptors of *Argopecten* (=Pecten) *irradians*. Membrane depolarization exceeds threshold and triggers a spike burst in the proximal receptor (A). Hyperpolarization inhibits ongoing spontaneous activity in the distal receptor followed by a burst of spikes with depolarization following light off. The inhibitory response is similar to the inhibitory model (Fig. 2). From McReynolds and Gorman (1970a).

Receptor physiology has been studied in the eyes of only a single additional bivalve species, the giant clam *Tridacna maxima* (Wilkins 1988). Although no recordings were made from optic nerve fibers, responses to light recorded intracellularly from retinal cells are hyperpolarizing, consistent with primary inhibition characteristic of bivalve photoreensitivity. Unlike the scallop, however, two types of inhibitory photoreceptors have been described, and no excitatory cells were found. Classified as spiking (S) and non-spiking (NS) receptors (Fig. 5), these cells can be distinguished by the following criteria. The S-cells, which share most of the characteristics of scallop distal photoreceptors, are hyperpolarized by light and spikes are suppressed. Similarly, light has a secondary excitatory effect seen in the strength of the spike burst arising

from the off-response depolarization. This is illustrated (Fig. 5A) where spikes are absent in the second off-response as a consequence of reduced light adaptation from the initial dark period, and where the number of spikes increases relative to increases in duration of the preceding period of illumination (Fig. 5B). Spiking in NS-cells has never been observed. It is possible that the absence of spikes is due to injury from electrode penetration, as has been reported commonly for both cell types in scallops (McReynolds and Gorman 1970a). However, S-cells retain their ability to conduct action potentials as long as cell penetrations are maintained, for periods up to an hour. Further, *T. maxima* receptors are invariably distinguished by differences in membrane potential and light adaptation. S-cell receptor

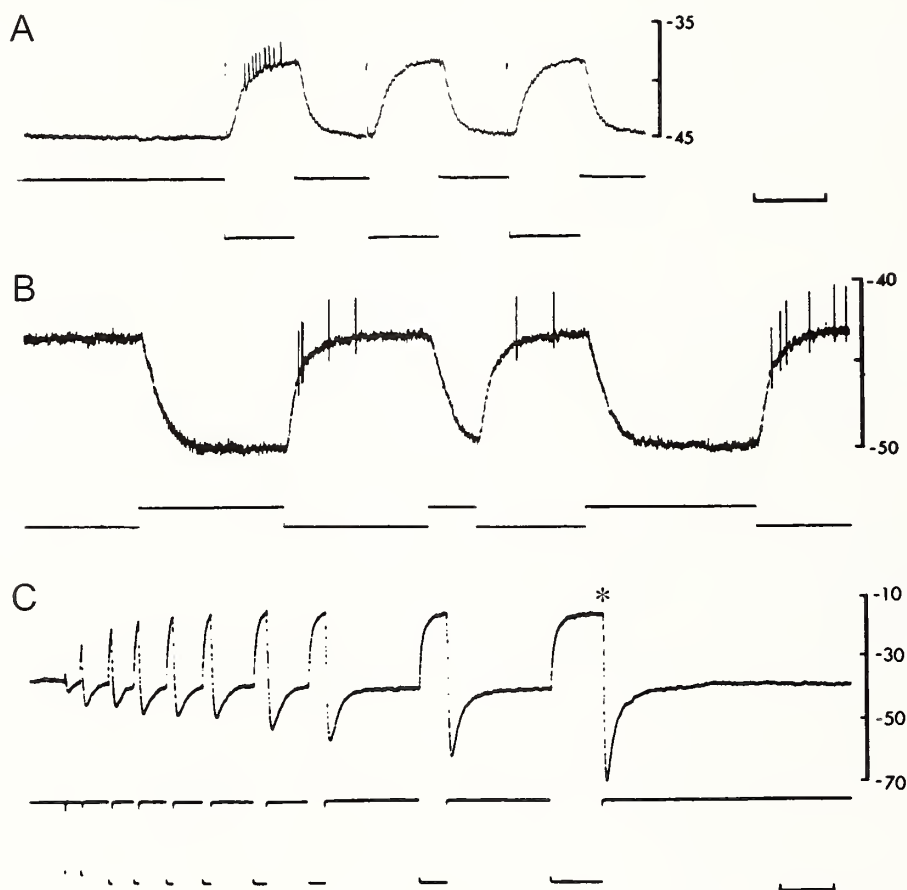


Figure 5. Receptor potential in *Tridacna* photoreceptors. Spiking S-cell off-response beginning when fully light adapted following several minutes under bright illumination (A) and beginning when fully dark adapted (B). The light-off burst of spikes is greatest for higher degrees of light adaptation, e.g., the initial dark period in (A) and spike counts in response to relative durations of light exposure in (B). Non-spiking NS-cell (C) beginning in a fully light-adapted state followed by shadow stimuli of increasing duration. Inhibitory hyperpolarization in response to light increases following increasing intervals of illumination. Relative light adaptation in S-cells is evident in the spike burst response but not in receptor potential amplitude, whereas NS-cell responses change dramatically with relative light adaptation. The light stimulus is monitored in the lower trace of each pair; light on is the upward position. Vertical scale indicates actual membrane potential in millivolts; horizontal bar = 30 s in (A) and (C), 5 s in (B). Modified from Wilkins (1988).

potentials are seemingly immune to adaptation, either in the light or in the dark (Fig. 5A-B), whereas the receptor potentials of NS-cells respond variably as a function of light exposure (Fig. 5C). At the beginning of this record (Fig. 5C), the cell is fully light adapted and inhibitory-like hyperpolarizations increase dramatically following increasing durations in the dark. On-response hyperpolarizations also adapt rapidly, returning to the light-adapted baseline irrespective of changes in relative dark adaptation as seen throughout this record. Membrane and receptor potentials also vary consistently, with average resting (dark) potentials of -44 mV in S-cells and -14 mV in NS-cells and hyperpolarizing off-responses averaging 14 mV or up to 100 mV in fully light-adapted S- and NS-cells, respectively. Both cell types have axons that emerge from the receptor soma, as seen in injections of fluorescent dyes following recording sessions (Wilkens 1988). These converge to form the optic nerve described morphologically by Stasek (1966) and Kawaguti and Mabuchi (1969). Neither Kawaguti and Mabuchi (1969) nor Fankboner (1981) report synapses in their electron micrographs of the *T. maxima* retina.

Receptor physiology, consistent in its inhibitory response to light, is nevertheless significantly different in the eyes of scallops and giant clams. Differences, as yet unexplained, also exist in the organization of the visual apparatus. The dual retinas in scallops form a common optic nerve that

projects without branching or synapse formation into the lateral (optic) lobes of the parietovisceral ganglion (Spagnolia and Wilkens 1983, fig. 6). Any mantle reactions to light are therefore dependent on efferent projections back to the periphery. In *Tridacna maxima* small pieces of mantle tissue, excised and pinned out for recording, exhibit local retractions to shadows. This requires that optic fibers synapse with other cells after leaving the eye capsule, or that dermal photosensitivity exists in the mantle aside from the eyes, as in *Lima scabra* (Mpitsos 1973). Receptor organization is also different, as histological studies in *T. maxima* do not show the distinct retinal layers characteristic of scallop eyes. *Tridacna maxima* receptor cells are described by Fankboner (1981) as having numerous ciliary processes that give rise to tangles of microvilli whereas Kawaguti and Mabuchi (1969) distinguish two cell types, one of which is described as rhabdomeric but having ciliary basal bodies. Both authors may be describing the same ciliary receptor somewhat differently, but no evidence as yet relates any structural difference to the physiologically distinct S- and NS-cells.

Contrasting ionic mechanisms of hyperpolarizing receptor potentials

The receptor potentials and mechanisms of phototransduction in scallops have been studied extensively with respect to their differing polarity. In *Argopecten irradians ir-*

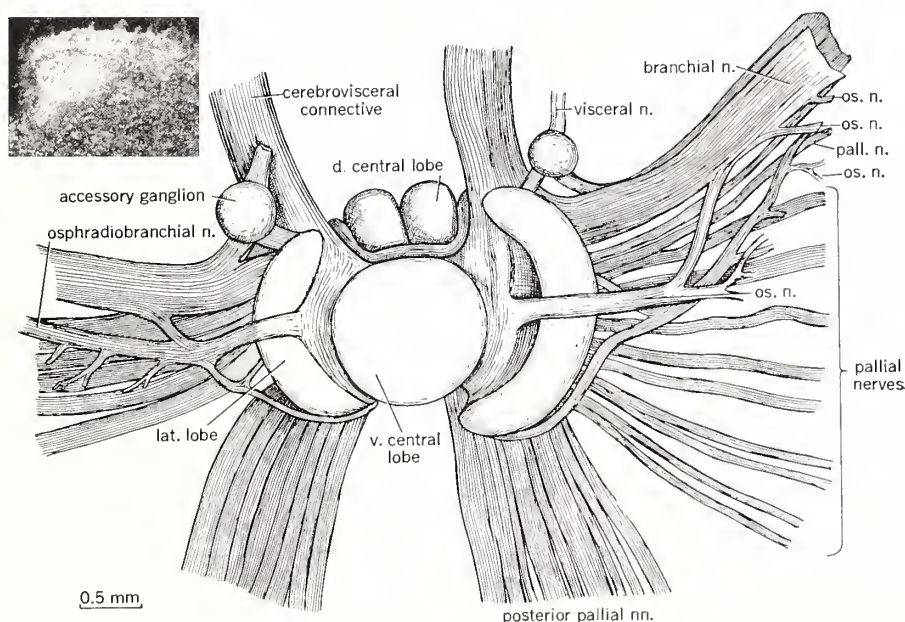


Figure 6. Diagram of the parietovisceral ganglion of *Pecten*. From Dakin (1910). The larger lateral lobe on the right corresponds with the upper (left) mantle that contains a larger number of eyes than present on the lower (right) mantle. The inset (Wilkens, unpublished) shows autoradiographic labeling of cortical neurons (surface layer) and a spherical glomerulus after injection of tritiated proline into the eye and axonal transport via the pallial nerves into the lateral lobe.

radians, both depolarizing and hyperpolarizing receptor potentials are based on increases in ionic conductance (McReynolds and Gorman 1970b). The excitatory depolarizing potentials of arthropods, and presumably other invertebrate photoreceptors, also arise from increases in membrane conductance (Fuortes 1959), whereas in vertebrate receptors the 'inhibitory' hyperpolarization is associated with a decrease in conductance (Toyoda *et al.* 1969). Therefore, receptor polarity and conductance changes must be explained as a function of ion channel specificity. In scallop proximal receptors, an increase in inward sodium conductance drives the excitatory depolarization (Gomez and Nasi 1996), similar to other depolarizing receptors. In the distal receptors of scallops, which have received the greatest attention, hyperpolarization is due to an increase in outward potassium conductance (Gorman and McReynolds 1978), with similar ion specificity in *Tridacna maxima* (Wilkens 1988). These experiments are based on ion substitution and reversal potential measurements, with similar results in scallops and giant clams. However, hyperpolarizing light inhibition, as seen in bivalve photoreceptors and in vertebrate rods and cones, is based on contrasting mechanisms. In bivalves, hyperpolarization is due to an *increase* in conductance, *i.e.*, outward potassium current. In vertebrates, hyperpolarization is due to a *decrease* in conductance shutting off the leaky, inward sodium currents that depolarize the cell in the dark. Thus, the inhibitory effects of light are explained ultimately by ion channel specificity and its activation or suppression by the photochemical mechanisms following light absorption. For the scallop distal photoreceptors, as in vertebrates and other animals, much additional work has been directed towards understanding the cascade of second-messenger intermediates (Gomez and Nasi 2000), the evolutionary history of opsin photopigments, and their control of membrane conductance, and bivalve photoreceptors remain of great value in the comparative study of phototransduction.

Historically, the evolution of the eye has been of immense interest, including the morphology of its light-sensitive cells. Photoreceptors generally involve an extensive membrane hypertrophy involving either the cilium or microvilli of the cell membrane in the formation of a rhabdom. Aside from the competing theories concerning the phylogenetic relationships of photoreceptor morphology, some trends are in evidence physiologically. For example, all depolarizing/excitatory photoreceptors are exclusively rhabdomeric, including the examples mentioned previously, *e.g.*, all arthropods, annelids, gastropods, cephalopods, and the proximal receptors in pectinid eyes. In contrast, hyperpolarizing photoreceptors are predominantly ciliary although the list is fairly short, *e.g.*, vertebrate rods and cones, the distal photoreceptors and siphon/mantle nerves in bivalves, and

the photoreceptors in the larval eyes of the tunicate *Amauroucium constellatum* (Gorman *et al.* 1971). A lone exception is found in the eye of another tunicate, *Salpa democratica*, where the hyperpolarizing response is associated with a microvillar-type receptor although these eyes are considered non-homologous to those of other primitive chordates (Gorman *et al.* 1971). In another exceptional instance, a putative ciliary photoreceptor is found in the brain of the polychaete annelid *Platynereis dumerilii* (Arendt *et al.* 2004) although its response to light is unknown. Ciliary opsin similar to that of vertebrate rods and cones is associated with these photoreceptors but not the rhabdomeric receptors of the eyes.

Despite these trends, information is insufficient for linking physiological sensitivity to the evolution of photoreceptor morphology. Hyperpolarization is seemingly a characteristic of all chordate photoreceptors, as it is in bivalve eyes. However, the ionic and conductance mechanisms are distinctly different between these two groups. In addition, the depolarizing excitatory receptors of scallops are anomalous considering the bivalve emphasis on primary inhibition. Genetic analysis of the various phototransduction mechanisms is the likely avenue for resolving the evolutionary relationship of photoreception among animals. Nevertheless, further sampling of the physiological properties of bivalve eyes would be of great utility in understanding visual function in this sedentary group, including both cephalic eyes in the Arcoidea and Pterioidea and the rich diversity of pallial eyes, as reviewed by Morton (2001).

Behavioral implications from receptor physiology

The evolution of an inhibitory light response restricted to just two groups of unrelated animals makes for interesting comparisons. Inhibition in vertebrates must be viewed in the context of a complex retina with an extensive set of integrative components underlying image formation and dependent on the functional specificity of synaptic contacts from rods and cones to their post-synaptic targets. Transmitter release from receptors in a depolarized state is high while in the dark. With hyperpolarization transmitter release is reduced. However, the 'inhibitory' light response can be interpreted as either inhibitory or excitatory postsynaptically, depending on the specificity of ion channel activation by the neurotransmitter. For example, light inhibition that suppresses the release of an inhibitory transmitter will result in excitation while suppression of an excitatory neurotransmitter will have a net inhibitory effect. These and other synaptic interactions are integral to the construction of receptive fields in elements of the retina that are essential for spatial imagery, along with focus of the lens.

In bivalve vision, inhibition by light is presented directly to the central nervous system as an inhibitory signal, *i.e.*, the

cessation of activity from optic (or pallial) fibers that would otherwise be excitatory. However, it is generally accepted that a photoreceptor inhibited by light at a low-threshold, but also primed by a latent light-mediated excitation, is physiologically efficient for responding to a shadow (Land 1966), where spikes are triggered with minimal delay on the rising phase of the receptor potential (McReynolds and Gorman 1970a). Thus, bivalves have encoded response properties optimized for detecting shadows directly into their sensory receptors. In doing so, they avoid delay intervals inherent in the synaptic activation of second-order neurons for mediating an off-response, as is the case for the shadow response in barnacles where the effect of light is excitatory at the receptor level (Gwilliam 1963).

Light inhibition and the ensuing off-response in distal receptors is also optimal and potentially most important for signaling motion sensitivity. The distal retina lies in the image plane of the mirror-like optics of the scallop eye (Land 1965) and the off-response receptors are therefore shadowed or illuminated sequentially by movements in the visual field. A moving object whether light or dark is an effective stimulus since movement will invariably darken some part of the retina (Land 1966). The excitatory receptors in the proximal retina lie outside the image plane, lack spatial acuity, and also adapt rapidly to light (McReynolds and Gorman 1970a) and under lighted conditions would be less responsive to rapid increases or decreases in light intensity. Thus, the more phasic off-receptors inhibited by light are optimally designed and positioned in scallops to detect movement, signals that represent potential predators for a sedentary animal, swimming not withstanding. Off-receptors perform the same function in the giant clam although without the benefit of an image-forming mirror in what Stasek (1965) refers to as the 'sight reaction'. Movements in the environment trigger rapid mantle retraction and valve adduction without shadowing to avoid the potential grazing of predatory reef fish. Spatial resolution is limited to that provided by the aperture of the invaginated pinhole eye, but Land (2003) has nevertheless measured acceptance angles for individual receptors that correspond to the motion-induced behaviors. Primary inhibition in bivalves can therefore be viewed as an evolutionary adaptation for survival, whether for responding to a shadow by animals lacking eyes or responding to movement in the environment. Movement detection has been likened to the function of a burglar alarm (Nilsson 1994), giving the animal advance warning not available to animals lacking eyes and dependent on shadows.

Nevertheless, many aspects of bivalve vision remain poorly understood, including whether or not eyes are essential given that the vast majority of species have no eyes (Morton 2001). At the opposite extreme, the ark clams have hundreds of eyes. Also, there is great diversity in eye mor-

phology among the species where eyes do exist (Nilsson 1994, Morton 2001) and physiological information is lacking except for the handful of species discussed here. Indeed, it is an open question whether eye diversity is homologous (Nilsson 1994) so receptor physiology could provide additional insights concerning the evolution of bivalve vision.

Aside from the burglar alarm theory, what function do eyes provide? In addition, what is the function of the depolarizing on-receptors found so far only in scallops and the file clam? Despite the evidence for image formation in scallops there is little indication that images are useful, other than for motion sensitivity, and doubt exists as to whether the central nervous system has the computational machinery required to process an image (Morton 2001).

The functional morphology of eyed bivalves still invites inquiry into the question of spatial vision. In scallops, for example, optic tracts entering the parietovisceral ganglion via the pallial nerves innervate the lateral lobes, the functional equivalent of 'optic' lobes (Fig. 6). Optic fibers make initial synaptic contact with a cortical layer of second-order neurons that in turn communicate with glomerular structures deeper into the optic lobes (Spagnolia and Wilkens 1983). Simple methylene blue staining of live tissue shows that the lateral lobes contain numbers of glomeruli in proportion to the eyes in the mantle, and in the diagram of the *Pecten maximus* ganglion (Fig. 6), the larger size of the left lobe reflects the greater number of eyes on the corresponding dorsal mantle. Glomerular structures are characteristic of high-level sensory integration so it is tempting to speculate that these structures make use of neural images from the eye. Curiously, however, in recordings from the cortical surface of the lateral lobes in *Euvola* (= *Pecten*) *ziczac* (Linnaeus, 1758), light stimuli elicit far greater activity from second-order visual neurons associated with on-responses in the optic nerves than for off-responses (Wilkens and Ache 1977). This suggests a high degree of input from the depolarizing proximal receptors although their 'unfocused' role has been suggested as being limited to detecting only changes in overall light intensity. New evidence (Speiser and Johnsen 2008) that both retinal layers receive focused images from the optical mirror is consistent with the predominance of excitatory input centrally. Visual function in scallops remains as an interesting avenue for further research.

Vision, when present in bivalves, involves numerous eyes distributed around the mantle/shell margins of the animal with numbers ranging up to hundreds in arcaceans. In the ark clams, pigment-cup and compound eyes are present, both in high numbers but with poor resolution (Nilsson 1994). The large number of eyes and even larger number of ommatidia are well designed to function as an alarm system with a high safety factor estimated at up to 755 receptor units for any direction in the visual field (Nilsson 1994). The

visual system of *Tridacna* is also comprised of a large number of eyes, and with a high degree of overlap considering the scalloped arrangement of the mantle lobes and radial orientation of the eyes plus an acceptance angle for individual receptors estimated at 16.5° (Land 2003). In essence, all of these visual systems have the potential to form a mosaic type of image projecting to the central nervous system. Even animals without eyes nevertheless are able to form a diffuse spatial image, as demonstrated in echinoids based on their orientation and movement toward large contrasting objects (Blevins and Johnsen 2004). Scallops have functional optic lobes, but very little is known for other bivalves about visual integration or the functional morphology for vision in the central ganglia. Visual behavior in giant clams suggests at least the possibility that a coarse visual image of the environment can be constructed. Stasek (1965) notes anecdotally that *Tridacna* has been observed to aim the exhalant cone at objects held over the mantle, much as they do when spurting water in the direction of mantle irritants, e.g., a grazing reef fish. While this behavior has not been confirmed, valve adduction and mantle retraction responses in these clams have been shown to habituate to a moving shadow presented repetitively in one part of the visual field but remaining responsive to a novel motion stimulus in another area (Wilkens 1986). In one instance, a giant clam habituated in this fashion responded vigorously to the shadow of a passing cloud. These behaviors suggest that some degree of discrimination for objects or movement in the visual field exists and that this capacity requires a type of collective image formation centrally. It remains that bivalves, as a largely sedentary group of animals, have at best limited needs for a sensory system with high visual acuity. Nevertheless, the 'evolutionary energy' in developing functional eyes and a behavioral repertoire in a few species challenges us to explain the adaptive significance of these visual systems. This is especially true for the scallop and file clam where both inhibitory and excitatory photoreceptors are present and the animals are capable of locomotory responses.

ACKNOWLEDGMENTS

The symposium "Molluscan models: Advancing our understanding of the eye" was funded by grants from the National Science Foundation (NSF) (DEB 0614153) and the American Malacological Society (AMS) to Jeanne Serb.

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Submitted 19 October 2007; **accepted**: 30 July 2008; **final revisions received**: 2 October 2008